

Macadamia domestication in Hawai‘i

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Abstract Macadamia is one of the few international food crops domesticated from the Australian flora. It was first described in Australia in 1857, but developed as a crop in Hawai‘i following the First World War. Hawai‘ian cultivars are responsible for the majority of the world production. This study reviews literature and archival documents to clarify the domestication pathway of this germplasm. Uncertainty about the accepted wild origin of the Jordan introduction, believed to be the main source of Hawai‘ian cultivars, is highlighted. An unrecognised additional early introduction of *M. integrifolia* is identified, but its relevance to commercial germplasm is unknown. The Hawai‘ian industry preference for *M. integrifolia* germplasm may have arisen because the kernels used to evaluate this species were sourced from poorly managed orchards. There is strong evidence that *M. ternifolia*, which produces bitter kernels, was also introduced at some stage. The advent of vegetative propagation was a major event supporting domestication. The origins of all named cultivars have been clarified and the similarity of two, *Keaau* and *Mauka*, has been highlighted. The pedigree of advanced generation selections is clarified indicating *Keauhou* was a common maternal parent. These results add to

the heritage of the plant in both Australia and Hawai‘i. In addition, knowledge of the pedigree of advanced selections can be used to improve prediction accuracy in analysis of breeding trials. Finally, improved knowledge of the domestication pathway will assist ongoing conservation and genetic improvement of the genus.

Keywords Australia · Breeding · Ethnobotany · Grafting · Hawaii Agricultural Experiment Station (HAES) · “Rough-shell” macadamia · “Smooth-shell” macadamia

Introduction

Macadamia is widely recognised as the world’s premium nut (Hardner et al. 2009; Stephenson 2005). Kernels are consumed as roasted snack food, chocolate enrobed confectionary, an ingredient in bakery or ice-cream, and cooking oil. Oil extracted from kernels is also used for cosmetics. Macadamia kernels have a high market value per volume (Stephenson 2005) and may be stored without significant loss in quality after processing (Wall 2013).

Macadamia is the one of the few international food crops to have been developed from the Australian flora (Hardner et al. 2009). Four species of *Macadamia* F. Muell. are currently recognised (Mast et al. 2008): *M. integrifolia* Maiden et Betche and *M. tetraphylla* LAS

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Johnson that produce moderate sized (1–2 cm diameter) edible kernels; and *M. ternifolia* F. Muell. and *M. janseni* C.L. Gross et P.H. Weston that produce smaller (<1 cm) kernels which are not palatable due to high cyanoglucoside content (Hardner et al. 2009). Macadamia occur in the subtropical rainforest of eastern Australia (Hardner et al. 2009; Powell et al. 2014). *M. integrifolia* is distributed from the Numinbah Valley in the South, northward to the lower Mary River south of Maryborough, and *M. tetraphylla* grows from the Richmond River east of Casino north to the Coomera and Nerang rivers. The distribution of *M. ternifolia* is partially sympatric with most of the northern range of *M. integrifolia* from Samford Valley in the south to Gympie in the north. A single population of approximately 30 individuals about 150 km north of the distribution of any of the other species defines the natural distribution of *M. janseni* (Gross and Weston 1992; Shapcott and Powell 2011). Commonly, *M. integrifolia* is referred to “smooth shell”, in contrast to the “rough shell” *M. tetraphylla*.

The first domesticated macadamia is likely to be a tree that was planted in the Brisbane City Botanical Gardens in 1858 by Walter Hill, the then superintendent of the Gardens (McConachie 1980). Walter Hill also collected the specimens used to initially describe the genus (Hardner et al. 2009; McConachie 1980; von Mueller 1857). From the 1860s, macadamias were planted as ornamentals, coincident with the natural distribution of the species, and the first seedling orchard was planted at Rous in northern NSW sometime between 1878 and 1888 (McConachie 1980).

Despite the Australian origins of the plant, initial large-scale commercial development of macadamia occurred in Hawai‘i (Hardner et al. 2009; Moltzau 1939; Shigeura and Ooka 1984; Storey 1956; Wagner-Wright 1995). Macadamia was originally introduced into Hawai‘i in the late nineteenth Century. The first seedling orchards were planted in the 1920s and 1930s, following a developing awareness of the palatability of macadamia kernels. With the advent of reliable grafting methods in the mid-1930s, seedling orchards (and other seedling plantings) were surveyed by the University of Hawai‘i (UH—with which the Hawaiian Agricultural Experiment Station, HAES, was merged in 1929) to select candidates for further testing and development as cultivars. Between 1948

and 1990, 12 named cultivars were released from the UH program. In addition, advanced selections from the program have also been planted in commercial orchards (Hardner et al. 2009). Germplasm developed in Hawai‘i is planted extensively in Australian, Brazilian and South African orchards, and is the major source of the current world production of macadamia (Hardner et al. 2009).

Given the considerable reliance of the world macadamia industry on cultivars developed in Hawai‘i, it is important to develop a deeper understanding of the domestication pathway of these cultivars to identify gaps in the current domesticated germplasm and possible sources of elite germplasm for future breeding efforts, and to add to the heritage of this plant in Australian and Hawai‘i. However, knowledge of the domestication pathway of the Hawai‘ian cultivars is incomplete including: details of the individual seed-lots introduced into Hawai‘i, the origin and contribution to the domesticated germplasm of these introductions, and the lineage and relationships among most of the Hawai‘ian cultivars and selections. These issues may be resolved in macadamia because domestication of macadamia has been relatively recent compared with many other horticultural crops, and, literature, archival material and oral history records are still available.

Introduction of macadamia into the islands of Hawai‘i

Purvis introduction

Several authors (Forbes 1928b; Hamilton and Storey 1956; Moltzau 1939; Shigeura and Ooka 1984; Wagner-Wright 1995) suggest William Herbert Purvis was the first to introduce macadamia into Hawai‘i. Purvis immigrated in 1878, and set up the Pacific Sugar Mill in Kukuihaele¹ in 1879, on the north-east coast of the big island of Hawai‘i (Dorrance 2001). Purvis was also responsible for introducing cinchona and the first mongooses into Hawai‘i (Wagner-Wright 1995).

Storey (1977) reports Purvis introduced macadamia into Hawai‘i in 1878, although, it seems unlikely

¹ Orthography of Hawai‘ian places named taken from: Pukui M.K., Elbert S.H., E.T. Mookini 1974. Place names of Hawaii. University of Hawaii Press. Honolulu.

Purvis would have brought material with him when he first travelled to Hawai‘i. Others suggest 1881 (Shigeura and Ooka 1984; Storey 1956), 1885 (Hamilton and Storey 1956; Storey 1965; Thevenin 1961), or sometime between 1881 and 1885 (Hamilton and Fukunaga 1962a). David Forbes (1928b) suggests the Purvis trees appeared to be 5–6 years old when observed in 1887, suggesting if macadamia was introduced as seed this may have occurred earlier than 1883.

Some authors (Forbes 1928b; Hamilton and Fukunaga 1962a; Moltzau 1939) suggest the macadamia introduced by Purvis were planted in the garden of his house at Kukuihaele on the island of Hawai‘i. Others (Shigeura and Ooka 1984; Thevenin 1947; Wagner-Wright 1995) suggest the Purvis trees were planted at Kapulena, approximately 5 km south-east of Kukuihaele.

The Purvis introduction is believed (Shigeura and Ooka 1984) to have been predominately *M. integrifolia*. Some authors (Moltzau 1939; Moltzau and Ripperton 1939; Shigeura and Ooka 1984) argue the introduction also included *M. ternifolia*, as the raw kernels produced by these trees are described by Forbes (1928b) as small with an unpleasant (but not ‘bitter’, as suggested by Pope 1929b; Shigeura and Ooka 1984) flavour. Forbes (1928b) also mentions the kernels were palatable, which would be unexpected for those produced by *M. ternifolia*.

The source of the Purvis germplasm is unknown. Moltzau (1939) reports that the nuts were given to William Purvis by his brother, an Admiral Purvis (no initials given), however, no records could be found of this relation. Hedemann (1994) suggests Purvis collected macadamia when he visited Sydney in mid-1883 for a month, after travelling from Ceylon (where he collected cinchona and tea) on the SS Australia.² Alternatively, Purvis himself³ indicates that when he left England to return to Hawai‘i in late 1882, he took a gardener and Wardian cases of plants for Hawai‘i. McConachie (1980) suggests the Purvis introduction came from Mt Bauple, although no justification for this is given.

² Purvis W.H. 24th March 1929 unpublished notes concerning time spent at Kukuihaele, Hawai‘i, during the years 1879–1882: held by Kona Historical Society, Hawai‘i.

³ Purvis *Op. cit.*

Jordan introduction

The second introduction of macadamia into Hawai‘i is attributed to the brothers Edward W. and Robert A. Jordan in 1892 (Connell 1933; Hamilton and Storey 1956; Higgins 1920; Moltzau 1939; Pope 1929b; Thrum 1928). Many reports (Hamilton and Storey 1956; Moltzau 1939; Shigeura and Ooka 1984) indicate the Jordan introduction was *M. integrifolia*. It is suggested (Pope 1929b; Shigeura and Ooka 1984) Robert Jordan sent seed from Queensland to Edward who planted the trees raised from these seed on his property in Nu‘uanu Valley, Honolulu. Beaumont (1956) suggests the origin of the seed was from the south of Brisbane. However, 2 years later, he suggests (Beaumont 1958) the introduction was sourced from the Brisbane region, in part, because progeny from the Jordan introduction did not appear to produce the range of superior kernels that were produced by germplasm derived from the northern range of the species around Amamoor and Imbil.

Lowndes (1966) may have been the first to suggest the Jordan introduction was sourced from a farm at Hotham Creek, south of Brisbane owned at the time by Francis Lahey, reporting that “a Captain Jordan visited his friend’s farm” at this location. Others (McConachie 1980; Wagner-Wright 1995) report “Captain Jordan” was an Irishman who was first mate on a sailing vessel that had berthed in Brisbane and travelled to the farm where he was given a sugar bag half full of nuts. This account is supported by Shirley Lahey, granddaughter of Francis Lahey (Shigeura and Ooka 1984), but is in conflict with other information about Robert Jordan. Other records (Shigeura and Ooka 1984; Siddall 1917)^{4,5,6} indicate R.A. Jordan was a bookkeeper for his brother E.W. Jordan in Hawai‘i in 1898, was born in Bedfordshire England in 1842, moved to Queensland in 1861, married in 1867, sired 6 children in Australia between 1868 and 1881, was the manager of a large boot factory in Brisbane, and migrated to Hawai‘i in 1896. These

⁴ Anon. 1898: Husted’s Directory and Handbook of Honolulu and the Hawai‘ian Islands. Page 122. (<http://evols.library.manoa.hawaii.edu/handle/10524/35849>. Accessed 23/9/2014).

⁵ Birth and Marriage records, Queensland State Archives (<https://www.qld.gov.au/law/births-deaths-marriages-and-divorces/family-history-research>, accessed 23/9/2014).

⁶ Passenger manifests held by Hawai‘ian State Archives.

inconsistencies question whether the Jordan introduction into Hawai‘i is derived from Hotham Creek.

Territory Board of Agriculture and Forestry *M. tetraphylla* introduction

Six trees of *M. tetraphylla* were planted by the Territory Board of Agriculture and Forestry between 1892 and 1894, at an elevation of 1000 ft. as part of reforestation plantings of the slopes of Mt Tantalus on the island of O‘ahu (Hamilton and Fukunaga 1962a; Hamilton and Storey 1956; Higgins 1918, 1920; Moltzau 1939; Pope 1929b). Three of the trees were planted on the land of Kewalo-uka, set aside by the then Hawai‘ian government as the location of an agricultural experiment substation (Pope 1929b). This land was transferred to the HAES in 1900, and developed as the Tantalus substation (Crawford 1937; Hamilton and Fukunaga 1962a). The other three trees were planted on an adjoining Territorial forest reserve as parcel boundaries were not well defined at the time (Pope 1929b).

Little is known of the source of this introduction (Beaumont 1956). McConachie (1980) suggests the seed may have been collected by American botanists visiting Australia in 1892. It is also suggested (McConachie 1980; Storey 1957) the collection may have been from a single tree which Dr. J.H. Beaumont (UH) reportedly (Storey 1957) located when he visited Australia in 1953.

The trees flowered in 1908 (Pope 1929b) and produced seed from 1917 (Higgins 1918; Westgate 1921b). In 1922, about 50 seedlings that had been propagated from seed collected from the original trees were planted at the substation (Pope 1923, 1927).

Other introductions

Several authors (Pope 1929b; Storey 1956; Thevenin 1947) report additional early introductions of macadamia seed into Hawai‘i were made by other individuals and the USDA. Forbes (1928b) reports a large scale introduction around 1911/12, and indicates he had planted some of the trees on his properties south of Hilo, and at Waimea, on the island of Hawai‘i (see also Shigeura and Ooka 1984). Others⁷ confirm the

material planted by Forbes at Waimea was from a different source to the Purvis and Jordan introduction. It is unknown if this introduction was related to a consignment of 10,000 macadamia seeds sent from Australia to the USDA by Herbert Rumsey in 1912, from which trees were propagated and planted out in California, Texas and Florida (Rumsey 1927). A planting of macadamia on the island of Maui by Dr. David Starr Jordan in 1887, which due to its time of planting may represent another early introduction of macadamia, is reported by Wagner-Wright (1995), but this has not been verified.

In 1927, UH introduced a small seed lot of macadamia from Queensland, but none of the seed germinated (Pope 1928b). However, additional introductions made in 1931 were successfully propagated and planted at the UH Kainaliu-Kona Experiment Station (Pope 1932). No further information on the source of these introductions was found.

Seeds were also imported by the Honoka‘a Sugar Company (HSC, had established seedling orchards over a decade prior, see discussion below) and UH from W.R. Petrie in Australia in 1936 or 1937, under the names *Eggshell*, *Pearl*, *Venus* and *Comet*—names used by Petrie for his seed parents (Beaumont 1958; Storey 1963; Thevenin 1947; Wagner-Wright 1995). Selections *Comet*, *Rough King*, *Venus* and *Pearl* from the (Petrie) Yebri nursery were noted in the 1936 selection records.⁸ Presumably, these were scions collected from the parents of the seed lots introduced by HSC and UH. These selections were apparently introduced to investigate reported high kernel recovery (Anon 1937), however, the scions failed to grow (Storey 1963).

Between 1938 and 1977, 19 introductions of macadamia were recorded by UH (Table 1). Two seed sources *S1* and *S2* were supplied by W.A.T. Summerville who was an entomologist with the Queensland Department of Agriculture and Stock around this time (Summerville 1935). Presumably, these were the two seed introductions referred to in Anon (1939). A third introduction in 1938, was of seed from another of W.R. Petrie’s seed parents, *Eggshell* (Hardner et al. 2009; Storey 1963), possibly stimulated by the interest in finding thin shell varieties as shell

⁷ Thevenin L. 17th June 2014 personal Communication Puako.

⁸ UH macadamia selection records. Held by UH Hilo.

Table 1 Details of introductions of macadamia into Hawai'i by University of Hawai'i between 1938 and 1977, taken from University of Hawai'i plant introduction records held by University of Hawai'i, Hilo

Date	Description	Source
Aug 1938	Macadamia seed, var. S1 & S2	W.A.T Summerville, Nambour QLD, Aust
21st Nov 1938	100 eggshell nuts	W.R Petrie, Nutland Plantations, Petrie QLD, Aust
23rd March 1939	5 <i>M. whelanii</i> nuts ^a	W.A.T Summerville, Nambour, QLD, Aust
2nd Sep 1949	Macadamia scions	Andrew Jackman, "Lu-lilli-nuts" Buderim, QLD, Aust
25th Feb 1952	Scions of Aust selections, B5, J6, B6	A.A. Rose, QLD Dept Ag and Stock, Aust
22nd Feb 1954	Seed from single tree, believed to be hybrid	Collected by J.H. Beaumont, sent from SE QLD, Aust
22nd Feb 1954	<i>Macadamia praealta</i> seed ^b	Collected by J.H. Beaumont in QLD, Aust
29th Mar 1954	Seed identified as N27	R. Kebby University of Queensland, sent by JH Beaumont from QLD, Aust
30th Apr 1954	<i>M. whelanii</i> seed ^a	Brought back by J.H. Beaumont from QLD, Aust
30th Apr 1954	26 scions, HAES 671–697	
5th Oct 1954	Seed of <i>M. whelanii</i> ^a	S.E. Stephens Dept Ag & Stock, Nth QLD, Aust
8th Aug 1957	Scions of D1 <i>M. tetraphylla</i>	M.V. Montgomery Dept Ag and Stock, Maryborough, QLD, Aust
8th Aug 1957	Seeds of #74 macadamia (thought to be hybrid)	Lush Estate Vista, Calif. Sent by Bill Storey UCR, Calif., USA
6th Feb 1963	Macadamia var. "Porky"	Mr. Paul Thomson, Bonsall Calif., USA
15th Feb 1965	<i>M. hildebrandii</i> ^a	Indonesia
30th Nov 1970	<i>M. neurophylla</i> ^c	Dr. H.S. McKee, Dept Forestry, Noumea, New Caledonia
1st Jun 1976	<i>M. tetraphylla</i> Probert #1 & Probert #2	W.B. Storey, UCR, Calif., USA
31st Oct 1977	Unidentified macadamia species	Ian McConachie Nutta Products, QLD, Aust
31st Oct 1977	<i>M. integrifolia</i> seedling	from D. Bruce Coolaabin Nursery via Yandina, QLD, Aust

^a *M. whelanii* F.M. Bailey and *M. hildebrandii* Steenis transferred *Lasjia* Weston et Mast (Mast et al. 2008)

^b *M. praealta* F.M. Bailey transferred genus *Floydia* L. Johnson and B. Briggs (Johnson and Briggs 1975)

^c *M. neurophylla* transferred to *Vrotia* L. Johnson and B. Briggs (Johnson and Briggs 1975)

thickness was considered a major issue for cracking (Higgins 1920; Wagner-Wright 1995).

The first successful introduction of scion wood from Australian (*M. tetraphylla*) was in 1949 (Table 1) (Hamilton 1960). However, while the grafting was successful, these introductions reportedly (Hamilton 1960)⁹ didn't bear any fruit. In 1951, Dr. N.F. Clements of UH introduced six Australian clones to the Kea'au orchard (Beaumont 1958; Hamilton 1960),^{10,11} but no record of these introductions were found.¹² In 1952, a further two *M. integrifolia*, and one

M. tetraphylla, scions were introduced (Table 1) (Hamilton 1960).¹³

In 1954, further introductions from Australia were made by Beaumont following an expedition to this country a year earlier (Storey 1965).¹⁴ The selections B5 and J6, initially introduced in 1949, were apparently reintroduced and UH plant introduction records¹⁵ indicate an additional 24 Australian scions (Storey 1965). However, others (Hamilton 1960; Hamilton and Fukunaga 1962b) report 34 scions were introduced by Beaumont in 1954, while 35 selections—made by Queensland and NSW state agencies

⁹ Hamilton R.A. 1962. Notes. A brief sketch on seedling selection work. Series No. AR14. Lyman Museum Archives.

¹⁰ Goto B. 1962 Director HAES UH, Notes. Series No AR14 Held at Lyman Museum Archives.

¹¹ Hamilton *Op. cit.*

¹² UH plant introduction records. Held at USDA-ARS Hilo.

¹³ UH macadamia selection records. *Op. cit.*

¹⁴ Hamilton *Op. cit.*

¹⁵ UH plant introduction records. *Op. cit.*

between 1948 (Hamilton and Fukunaga 1962b; Leverington et al. 1961) and 1952 (Hardner et al. 2009; Leverington 1962) and five additional selections made in Australia by Beaumont—are noted in the UH macadamia selection records¹⁶ for 1954. An additional 14 Australian selections are listed as selections in 1956/57,¹⁷ with another six listed in 1960. One of these later Australian selections not included in the UH plant introduction book¹⁸ was *NSW44* (allocated UH selection number 695), later named *Beaumont* in California (Storey 1965). Dr. W.B. Storey sent clones from Australia to Hawai‘i during his 1961 expedition.¹⁹ By 1961, a total of sixty-one Australian clones had been introduced into Hawai‘i (Storey 1965),²⁰ with 49 of these successfully propagated (Storey 1965). The introductions *B5* (*Rickard*), *B21* (*Teddington*), *Beaumont* and *NRG* are parents of UH selections²¹ (see later).

Commercial seedling orchards

Presumably because macadamia was new to western culture, there appeared to be little horticultural interest in the plant in Hawai‘i until the initial plantings started to bear fruit around 1910 (Crawford 1937; Pope 1928a, 1930; Thevenin 1947). The first suggestion of the commercial potential of macadamia in Hawai‘i appears to be from 1909 (Wilcox 1909). Small plantings of macadamia were made throughout Hawai‘i between 1900 and 1915, mostly as ornamentals or home plantings (Connell 1933; Forbes 1927; Hamilton and Fukunaga 1962a; Hamilton and Storey 1956; Higgins 1920; Krauss 1922; Storey 1956; Wagner-Wright 1995; Westgate 1921b). Macadamias were also used as windbreaks for sugar (Wagner-Wright 1995). The hardness of the shell, and thus the difficulty of extracting the valuable kernels, was recognised (Higgins 1918, 1920) as an early impediment to commercial development of the plant.

M. tetraphylla plantings around Kona district in the 1920s

Wagner-Wright (1995) suggests that HAES began introducing macadamia into the Kona district from 1912, however, other records indicate it was not until 1918–19 that HAES distributed approximately 1800 predominately *M. tetraphylla* seedlings propagated from seed collected from trees growing on the Tantalus substation mainly to Louis McFarlane of the Captain Cook Coffee Co and numerous tenants of Bishop Estate (through agent T.C. White) on the west coast of the island of Hawai‘i as a possible alternative or supplement to coffee (Crawford 1937; Hamilton and Storey 1956; Higgins 1918, 1920; Iwane 1962; Pope 1922, 1923, 1924, 1925, 1927, 1928b, 1929c, 1930; Storey 1956, 1977; Thrum 1928; Westgate 1921a, b). These were planted at elevations between 600 and 2100 ft. and on different soil types (Higgins 1920; Iwane 1962; Pope 1927; Storey 1956). Around this time, HAES also collaborated with growers on the other two largest islands (presumably O‘ahu and Kaua‘i) to plant macadamias (Westgate 1920). By 1926, some of these seedlings planted in 1918 by T.C. White at Kealakekua near Kona had commenced bearing (Pope 1927). However, interest in macadamia declined as coffee prices rose in the 1920s (Hamilton and Fukunaga 1962a; Iwane 1962) and the early plantings were abandoned or removed (Beaumont 1958).²² By the late 1930s, as *M. integrifolia* became the preferred species for production (Hamilton and Storey 1956; Wagner-Wright 1995), many of the remaining *M. tetraphylla* plantings in the Kona district were top-worked with smooth-shell scions or destroyed, although some still existed in 1951.²³

Hawaiian Macadamia Nut Company (HMNC)

Nutridge orchard

The first large scale commercial planting of macadamia in Hawai‘i was probably the Hawaiian Macadamia Nut Company’s Nutridge orchard, although there is some uncertainty about the exact date of the first

¹⁶ UH macadamia selection records. *Op. cit.*

¹⁷ UH macadamia selection records. *Op. cit.*

¹⁸ UH plant introduction records. *Op. cit.*

¹⁹ Hamilton *Op. cit.*

²⁰ Hamilton *Op. cit.*

²¹ UH macadamia selection records. *Op. cit.*

²² Fukunaga E.T. 1951. Macadamia nut culture in Hawai‘i. pp 31. Kona Macadamia Nut Club. Held by Kona Historical Society.

²³ Fukunaga *Op. cit.*

plantings of macadamia by HSC (see below). This orchard was planted by Edward van Tassel's Hawaiian Macadamia Nut Company (HMNC) on land leased from the Hawai'ian government below Round Top east of the city of Honolulu on the island of O'ahu. Some authors (Hamilton and Storey 1956; Moltzau 1968; Thrum 1928; Wagner-Wright 1995) suggest the orchard was planted in 1920, while others (Hamilton and Storey 1956; Shigeura and Ooka 1984; Thevenin 1961) report 1922. This apparent conflict may have arisen as the initial 1920 planting was unsuccessful, due to poor plant husbandry (Moltzau 1968; Wagner-Wright 1995) and the orchard was replanted in 1922, and completed by 1925 (Moltzau 1968). Some sources (Anon 1927; Hamilton and Storey 1956; Storey 1956; Thrum 1928)²⁴ report the area of the orchard was approximately 25 acres, although others (Shigeura and Ooka 1984; Wagner-Wright 1995) report 75 acres. The address of Nutridge is confirmed as 3280 Round Top Drive, Honolulu²⁵ with an area of 22 acres.²⁶

Most authors (Moltzau 1968; Shigeura and Ooka 1984; Wagner-Wright 1995) consider the Jordan introduction was the major source of germplasm for Nutridge, with minor contributions from the Purvis and *M. tetraphylla* introductions. Alternatively, others (Storey 1977; Urata 1954)²⁷ suggest the Jordan introduction was the only seed source used for Nutridge. A note "Tantalus substitution" made in the UH records²⁸ for selection 465 from Nutridge indicates that *M. tetraphylla*, most likely derived from Tantalus, was also planted. Further, selection 475 (also from Nutridge and later developed as the cultivar *Wailua*) was described as a hybrid (Hamilton and Fukunaga 1973). Top-working at Nutridge was undertaken in 1935, but was reportedly (Anon 1937) less successful than experienced with top-working in other orchards. Sometime between the late 1940s and 1960,

the Nutridge orchard was abandoned (Hamilton and Nakamura 1971; Moltzau 1968; Westree 1963).²⁹

Keauhou orchard

A second orchard was established by HMNC in 1924, on 100 acres of land leased from the Bishop Estate at Keauhou on the island of Hawai'i (Shigeura and Ooka 1984; Thrum 1928; Wagner-Wright 1995). The Bishop Estate is a portion of the estate of Princess Bernice Pauahi Bishop bequeathed for the support and education of aboriginal Hawai'ians through the Kamehameha Schools (Mitchell 1993).

The site for the orchard was reportedly (Forbes 1927) selected as it was similar to an existing orchard planted earlier by T.C. White of the Bishop Estate. Over 7000 *M. integrifolia* and *M. tetraphylla* derived seedlings were planted from 1925 (Shigeura and Ooka 1984; Wagner-Wright 1995). Most of the orchard had been planted by 1928 (Thrum 1928), and was completed by 1934.^{30,31}

Storey (1977) reports the Jordan introduction was the source of *M. integrifolia* planted in this orchard. The *M. tetraphylla* germplasm was derived either directly from the Tantalus planting or possibly from progeny of this introduction planted around Kona from 1918. According to Wagner-Wright (1995), the Keauhou orchard was almost *M. integrifolia* by 1944, suggesting most of the original *M. tetraphylla* trees had been either top-worked (Moltzau 1968) or removed.

The productivity of the Keauhou orchard was considered to be poor.^{32,33} By the 1940s, harvesting of seedling orchards had ceased as nut quality was highly variable, and the location was considered unsuitable for macadamia production.³⁴ Presumably

²⁴ Fukunaga *Op.cit.*

²⁵ <http://www.nps.gov/nr/research/index.htm>. Accessed 3/9/2013.

²⁶ In results from search for 3280 Round Top Dr at <http://gis.hicentral.com/FastMaps/ParcelZoning/>. Accessed 24th September 2014.

²⁷ Stewart K. Transcript of interview with Leon Thevenin and Hiroshi Ooka, 12/4/1989. Hawai'ian Macadamia Nut Industry records, series No AR14. Held in Lyman Museum Archives.

²⁸ UH macadamia selection records. *Op. cit.*

²⁹ Wagner-Wright S. Transcript of interview with Dr Richard Hamilton, University Hawaii. 16/7/1991. Hawai'ian Macadamia Nut Industry records, series No AR14. Held in Lyman Museum Archives.

³⁰ Goto 1962. *Op. cit.*

³¹ Takahashi 1993. *Op. cit.*

³² Ralph Moltzau personal notes held at Ka Hale Olinda, Maui.

³³ Takahashi 1993. *Op. cit.*

³⁴ Lau L. Transcript of interview with Dr. Richard Hamilton UH. 14th August 1989. Hawai'ian Macadamia Nut Industry Records, Series No. AR14. Held at Lyman Museum Archives, Hilo.

the lease to the Keauhou orchard was included in the sale of HMNC in 1954 (Moltzau 1968).

Honokaa Sugar Company (HSC)

There is some conflict about the year of the first planting of macadamia by HSC. Some authors (Hamilton and Storey 1956; Moltzau 1939; Storey 1956)³⁵ suggest these plantings started in 1916. However, others (Thevenin 1961, 1968; Wagner-Wright 1995) report the manager of HSC, Walter Naquin, became aware of macadamia in 1918, the seedling nursery to service the plantings was established by the company in 1918,³⁶ and records of HSC indicate the seedling orchards were planted from 1924 (Shigeura and Ooka 1984; Storey 1977; Thevenin 1968). Thevenin (1961) reports HSC first planted macadamia in 1918, but planting of orchards commenced in 1924. Most reports indicate HSC initially planted macadamia as part of a project of land marginal for sugar cane on the slopes of Mauna Kea on the island of Hawai‘i and were more intensively managed after the value of the crop was realised (Storey 1956). From 1923 to 1930, the HSC planted seedling orchards at Kapulena (125 acres), Kuku highlands (125 acres) and Waipi‘o Valley (24 acres) (Thrum 1928).³⁷

The main seed sources for the HSC seedling orchards were reportedly a tree from the Purvis introduction growing in the yard of Charles Williams (Storey 1977; Wagner-Wright 1995), and a tree planted on the grounds of the old St Louis College on River Street, Honolulu (Urata 1954). Likewise, others³⁸ suggest the lineage of cultivars selected from HSC orchards traced back to the Purvis introduction. However, Wagner-Wright (1995) reports trees—grown from seeds imported from W.R. Petrie in 1936—may also have been planted in the HSC orchards.

Other seedling orchards

Other early seedling orchards are recorded in the literature (Shigeura and Ooka 1984; Wagner-Wright

1995) and the selection records of the University of Hawai‘i.³⁹ These orchards represent additional utilisation of the early germplasm existing in Hawai‘i at that time.

Hawai‘i

A small orchard of seedling trees was planted by Dr Benjamin Bond on land opposite the Kalāhikiola Congregational Church, ‘Iole Kohala, reportedly (Shigeura and Ooka 1984) around 1922, the same year as the replanting of the Nutridge orchard commenced and prior to the generally accepted year planting of HSC orchard commenced (see above). The source of germplasm for this planting is unknown; however, observations of the morphology of the remnant trees in 2013⁴⁰ indicate the trees are derived from *M. integrifolia*. Wagner-Wright (1995) reports around the same time HSC was involved with growers in the Kohala district to develop the macadamia as a crop. It may be the seedlings for the Bond orchard were derived from germplasm supplied by HSC, possibly tracing back to the Purvis introduction, although this was not supported by others.⁴¹ In 1927, Leon Wishard planted some macadamia in Kohala (Shigeura and Ooka 1984), most likely with seedlings provided by HSC.⁴²

O‘ahu

Another of the early commercial macadamia seedling orchards was at Hō‘ae‘ae Ranch, Waipahu, owned by Mark and Lawrence Robinson (Bailey 1928; Forbes 1928a; Hamilton and Storey 1956; Pope 1929b; Shigeura and Ooka 1984; Thrum 1928). A total of 250 apparent *M. integrifolia* trees (6 acres) were planted in 1922 (Pope 1929b; Thrum 1928; Wagner-Wright 1995), around the same time as the second planting at Nutridge and prior to the planting of the HSC orchard. Forbes (1928a) reports the Hō‘ae‘ae Ranch orchard was the only producing macadamia nut orchard of any extent in Hawai‘i in 1928. Nuts from

³⁵ Fukunaga *Op. cit.*

³⁶ Stewart *Op. cit.*

³⁷ Stewart *Op. cit.*

³⁸ Hamilton *Op. cit.*

³⁹ UH macadamia selection records. *Op. cit.*

⁴⁰ Site visited by author 5th June 2013.

⁴¹ Thevenin L. 16th June 2014. Personal communication.

⁴² Hawai‘ian Sugar Planter’s Association Plantation Archives. Box 29, Folder 4. Held at Hawai‘ian Collection, UH Manoa. Viewed 13th June 2014.

this farm received first prize at the 1926 and 1927 territorial fairs (Thrum 1928). Three significant macadamia plantings on O‘ahu totalling 72 acres in 1937 were reported (Ripperton and Coulter 1939). These included Nutridge, an orchard about 2.5 miles east of Waimea Bay at an elevation of about 750 ft that may be the Hopper orchard in Thrum (1928), and a third to the west of Kunia Camp, Wahiawā at an elevation of approximately 1200 ft. However, there is no record in Ripperton and Coulter (1939) of a macadamia orchard in the area in which the Hō‘ae‘ae Ranch orchard was located, although the orchard was mentioned in the UH macadamia selection records⁴³ and by Beaumont (1939a) around this time.

Kaua‘i

Seedlings of *M. tetraphylla* were sent by HAES to Kaua‘i as early as 1920 (Westgate 1920). Commercial macadamia plantings on Kaua‘i was reported in 1933 (Connell 1933). Wagner-Wright (1995) reports approximately 230 acres of macadamia were planted between Wailua Homesteads and Kalāheo on Kaua‘i in the 1930s, although Ripperton and Coulter (1939) report plantings only around the Kalāheo Homesteads in 1937.

The first commercial orchard on Kaua‘i was probably the A.R. Glaisyer orchard at Kalāheo, planted between 1928 (Thrum 1928) and 1930 (Wagner-Wright 1995). Wagner-Wright (1995) indicates that 10 acres were under macadamia in 1930. No record of the germplasm used for this planting has been found. A second macadamia orchard was planted at Kalāheo by Francis Takahashi sometime between 1933 and 1937, with seeds purchased from Nutridge.⁴⁴

The Deschwanden orchard of 27 acres was reportedly (Wagner-Wright 1995) planted in the 1930s in Lāwa‘i Valley. The deed of sale⁴⁵ records a sale of 27 acres from Barrero to A.R. Deschwanden on 21st November 1933. The source of seeds is not reported; however, one possibility is that the seeds were sourced from Nutridge through Francis Takahashi whose orchard was 2.5 km to the south. Hamilton and Ooka

(1966) report this orchard was in poor condition when visited in 1948.

Wagner-Wright (1995) details several other seedling orchards planted on Kaua‘i that included a total of 100 acres by Bill Moragne between 1934 and 1935, on Grove Farm Company land between Hulē‘ia and Līhu‘e. In addition, small orchards were established by D. Arcia at Wailua Homesteads, M. Kawamura at Līhu‘e, K. Watanabe, F. Tanabe and W. Gregg, the manager of the Kaua‘i Pineapple Company in Lāwa‘i Valley, S. Momohara, N. Kimura, E. Sevick and the Waimea Dairy Company at Kalāheo, and Duvel at ‘Ōma‘o (Wagner-Wright 1995).

Maui

Crawford (1937) reports that macadamia had been commercially planted on Maui prior to 1927. An orchard of five acres planted by Dr. Baldwin near Ha‘ikū is reported in Thrum (1928). A macadamia planting at the Ha‘ikū Poultry Farm was sampled by UH in 1944.⁴⁶ A significant macadamia planting of 15 acres in the north-west of Maui to the north of the Honokōwai stream is reported in Ripperton and Coulter (1939). In addition, Dr. David Thomas Fleming reportedly⁴⁷ planted macadamia in the Honokahua Valley NW Maui between the 1920s and the 1950s.

Development of cultivars and other commercial germplasm

Prior to 1938, all orchards were established with seedlings (Beaumont and Moltzau 1937; Hamilton and Fukunaga 1962a; Hamilton and Storey 1956; Storey 1956; Storey and Hamilton 1954; Wagner-Wright 1995). The great increase in macadamia plantings from the late 1940s is attributed to the development of reliable vegetative propagation methods (Hamilton 1960; Hamilton and Fukunaga 1962a; Storey 1963, 1965)⁴⁸ that enabled elite scions to be selected so as to reduce the variability in productivity and quality of kernels produced by seedling orchards (Anon 1935,

⁴³ UH macadamia selection records. *Op. cit.*

⁴⁴ Takahashi 1993 *Op. cit.*

⁴⁵ Deed of Covenyance v1232, p38 & v1348, p122 Held by Hawai‘i State Bureau of Conveyancing, Honolulu.

⁴⁶ UH macadamia selection records. *Op. cit.*

⁴⁷ Pam Shingaki UH Maui 19th June 2013 Personal communication.

⁴⁸ Fukunaga 1951. *Op. cit.*

1936; Beaumont and Moltzau 1937; Crawford 1937; Hamilton and Fukunaga 1962a; Hamilton and Ito 1986; Hamilton and Storey 1956; Pope 1929c, 1931; Storey 1956; Storey and Hamilton 1954; Thevenin 1947).

Development of vegetative propagation technology

Research on vegetative propagation of macadamia was undertaken by UH from 1919 (Pope 1922, 1929b). However, reliable grafting technology was not developed until 1933 (Anon 1934; Pope 1929c). Macadamia was first successfully grafted by Ralph Moltzau in 1927/28, when a branch that had broken from a tree and been left for several days was used as scion wood (Hamilton 1960; Moltzau 1968; Pope 1929a; Storey 1965; Wagner-Wright 1995). Grafting technology was developed further by UH during the early 1930s, although the reasons for Moltzau's early success may have not been initially fully appreciated (McConachie 1980). Westgate (1931) reports that grafting had been mastered by HMNC, but UH had achieved limited success from using juvenile scion wood although about 40 % success was achieved using older wood. Grafting success by UH increased the following year to 80 % (Anon 1935), and success was declared in 1935 (Anon 1936). By 1937, the accumulation of starch was identified as the physiological mechanism that supported grafting success (Jones and Beaumont 1937; Jones and Storey 1937; Moltzau 1937). Reliable methods for budding were not developed by UH (Beaumont and Moltzau 1937).

The first grafted macadamia plants started to bear in 1931.⁴⁹ Grafted trees reportedly (Anon 1935; Hamilton and Storey 1956) commenced bearing about 6–7 years of age compared to 10–15 years for seedling trees, although Pahau (1937) suggests grafted trees could start bearing about 2 years after grafting.

Successful propagation of macadamia by cuttings was achieved in the late 1920s by J.H. Pauls, the manager of the Keauhou Orchard.⁵⁰ Pope (1929b) reports that UH was also successful with propagation through cuttings, although this was contradicted in a later report (Pope 1931). Further studies were

undertaken by UH in 1947–1949 (Storey and Hamilton 1948; Storey et al. 1951), with results described as 'erratic' (Storey 1963).

Top-working of existing seedling orchards with elite germplasm was proposed (Beaumont and Moltzau 1937; Moltzau 1937) as a means to improve the productivity of the existing seedling orchards. However, top-working was not as successful as those from grafting on to young seedling rootstocks (Anon 1937; Beaumont 1939b; Beaumont and Moltzau 1937; Hamilton et al. 1981; Moltzau 1937).

Preference for *M. integrifolia* germplasm

Up to the early 1930s, there was no particular preference for either species for macadamia production in Hawai'i (Moltzau 1968). Most of the early orchards in Australia were planted with *M. tetraphylla* germplasm (Hardner et al. 2009). However, as HMNC started to process nuts in the early 1930s, it reportedly (Wagner-Wright 1995) refused to purchase nuts from *M. tetraphylla* as the kernels were considered bitter, although this is not a trait normally associated with this species (Hardner et al. 2009). Experiments undertaken by UH in 1934 (Anon 1935; Moltzau and Ripperton 1939), suggested that "rough shell" (*M. tetraphylla*) nuts tended to be more variable and have a higher proportion of immaturity compared to kernels produced by "smooth shell" *M. integrifolia* trees. *M. tetraphylla* was the common nut in coffee groves around Kona up to 1936 and it is suggested (Anon 1936) that poor handling by coffee growers may also have contributed to the lower quality of kernels extracted from rough-shell nuts. In addition, the *M. tetraphylla* germplasm used in Hawai'i was apparently descended from a narrow genetic base of 6 trees and is unlikely to be representative of the variation available in the species. By 1936, UH was advising that *M. integrifolia* had become the favoured species for production in Hawai'i, particularly due to differences in quality among kernels derived from the different species (Anon 1936).

It is recognised that the *M. tetraphylla* germplasm initially introduced into Hawai'i in the late nineteenth century may have been from an inferior source (Beaumont 1958; Storey 1957). Hamilton and Fukunaga (1973) suggest that it may be possible to produce

⁴⁹ Goto 1962 *Op. cit.*

⁵⁰ Ralph Moltzau. Unpublished letters to the HMNC Board. Held at Ka Hale Olinda, Maui.

hybrids that combined the best characteristics of both species.

UH selection records

As the early seedling orchards began to come into production, the development of reliable methods for vegetative propagation of scions through grafting onto seedling rootstocks motivated UH from 1933 to survey existing trees to identify elite candidates (Anon 1934, 1935; Hamilton and Ito 1986; Pope 1931). By 1936, particular trees were being recommended for use as scions, predominantly for top-working (Anon 1936).

In 1936, Ralph Moltzau and M.L. MacDougal of UH, supervised by Drs. Beaumont and Storey, commenced a large scale survey of existing seedling orchards for elite seedlings (Beaumont 1937; Moltzau 1968; Storey 1963, 1965, 1968; Wagner-Wright 1995). Selection was based on tree growth and structure, bearing habits, suitability of nuts for commercial cracking including uniformity of size and shape, kernel recovery, and kernel size (Hamilton and Storey 1956; Storey and Hamilton 1948).

Approximately 15,000 seedlings of an estimated 60,000 growing in Hawai'i were surveyed in 1936 (Moltzau 1937; Storey 1948). Selections made following the initial screening were given a UH selection number.⁵¹ However, existing records⁵² of these selection numbers commence at 240 with 290 records (UH selection numbers: 240–549 with gaps) for 1936. Moreover, Moltzau (1937) reported a total of 320 selections for 1936, suggesting that the the UH selection records⁵³ may not include all selections made in 1936. Of the 290 records,⁵⁴ 124 were sourced from the Nutridge orchard and 116 from the Keauhou orchard. The high frequency of selections from these orchards may be in part due to the difficulty of travel around the islands in 1936.⁵⁵

Other sources of the 1936 selections include: Āhualoa Homesteads, mauka of Honoka'a, Arcia, Duval, Glaisyer and Lidgate on Kaua'i, Ha'ikū on

Maui, Haina near Honoka'a on Hawai'i (nine selections, with no information to indicate if this was an orchard or not), Waipi'o Valley (assumed to be the HSC orchard) on Hawai'i, an unknown location in Kona, one of the original trees planted by E.W. Jordan, Hō'ae'ae (possibly from the Hō'ae'ae Ranch Orchard or remnants thereof), Wahiawā on O'ahu, and four selections that were sourced from Yebri Nursery in Australia. Storey (1963) reports that at least two of the selections from Yebri produced thinned shelled nuts in Australia, but, as indicated above, the grafts by HAES of these selections were unsuccessful.

There are 70 selections recorded for 1937/38 (UH selection numbers: 550–619); again predominately from the Nutridge and Keauhou orchards.⁵⁶ Other sources of selections include some surveyed in 1936, and new orchards including the Bond orchard on Hawai'i, and from Fukuda, Gouvea, Hayashi, Kim, Koyana, Sakamoto and Wilcox.

Sixty-two selections were made between 1940 and early 1950s (UH selection numbers: 620–672), from the Deschwanden, Eckert and Takahashi orchards on Kaua'i, the Ha'ikū Poultry Farm, Baldwin Estate and Gilbert Maeda on Maui, the Taba and Okinaga orchards at Kona on Hawai'i, Pūpūkea on O'ahu, and two unknown locations.⁵⁷ One of the Jackman scions introduced from Australia in 1949 (see above), is also included in the selection records.

Fifty-seven of the 75 selections recorded between 1952 and 1957 (UH selection numbers: 673–746)⁵⁸ were introductions from Australia (although only 49 were successfully propagated in Hawai'i, see above). The Australian selection *NSW44* introduced into Hawai'i was given the UH selection number 695. There were also three introductions from California, and selections from the Momohara, Deschwanden and Takahashi orchards on Kaua'i, the Baldwin estate on Maui, Kunia Board of Forestry (presumably on O'ahu) and Higashi at Honoka'a. Some of these selections were made following resurvey of older seedling orchards (Beaumont 1958). In addition, *Smooth Queen*, a selection from the UH Kainaliu-Kona Experiment Station, and a *M. tetraphylla* selection from Kona (unknown if this was the UH Experiment

⁵¹ UH macadamia selection records. *Op. cit.*

⁵² UH macadamia selection records. *Op. cit.*

⁵³ UH macadamia selection records. *Op. cit.*

⁵⁴ UH macadamia selection records. *Op. cit.*

⁵⁵ Chase S. Transcript of interview with Mr. Yosoto Egami, 1st March 1990, Hawai'ian Macadamia Nut Industry records, series No AR14 Box 32 Folder 14. Held in Lyman Museum Archives.

⁵⁶ UH macadamia selection records. *Op. cit.*

⁵⁷ UH macadamia selection records. *Op. cit.*

⁵⁸ UH macadamia selection records. *Op. cit.*

Station) were recorded. One of Petrie's parent trees was named *Smooth Queen* (Hardner et al. 2009), and it may be that the UH selection with this name was a progeny from the Petrie seed-lots introduced by UH and HSC in the mid-1930s, particularly as Beaumont (1958) reported selections had been made from this germplasm.

A further 119 selections were made between 1960 and 1976 (UH selection numbers: 747–865).⁵⁹ Fifteen of these selections were introductions of Australian selections including *H2* (727), *NRG* (771), *Own Choice* (772) and *D4* (also known as *Renown*, 773) and others developed by Norm Greber. This information supports Peace (2005) who, using DNA marker analysis, independently suggested that selection 772 introduced from Hawai'i to Australia in the 1980s (Winks et al. 1987) was actually *Own Choice*. There were also nine introductions from California including *Hall* (730), *Burdick* (756) and *Faulkner* (778) and three from Brazil. Also included in this selection era was the selection 767, which was used to represent *M. tetraphylla* in a trial at UH Captain Cook Experimental Station comparing the effect of *M. integrifolia* and *M. tetraphylla* derived rootstocks.⁶⁰ The source was described as a 'Hō'ae'ae seedling' (presumably meaning the seed was collected from a plant in the Hō'ae'ae orchard) from the Mapulehu Valley, Moloka'i.

Ninety-six of selections between 1960 and 1976, were advanced generation open-pollinated (OP) progeny of earlier selections or released cultivars (Beaumont 1958). The first of these were planted between 1947 and 1948, at Helemano on O'ahu in cooperation with the Waialua Agricultural Company (Storey et al. 1951; Wagner-Wright 1995). The most common parents were *Keauhou*—246 (52 selections) and *Faulkner*—778 (12 selections). Parents of other selections included: *Ikaika*—333, *Jordan*—462, 489, 491, 503, *Keakea*—508, 511, *Keaau*—660, *Rickard*—666, *T28*—670, *Teddington*—685, *Beaumont*—695, *Jackman # 1*—718, *NRG*—771, 777, 787, *Pāhala*—788 and *Honoka'a Special*. It has been estimated (Hamilton and Ito 1976, 1986) more than 100,000 seedlings were examined and evaluated between 1936 and 1976.

From 1977, 48 selections were recorded (UH selection numbers: 866–914) with 1981 the last recorded year.⁶¹ Of these selections, 10 were from seedling trees planted at the Kea'au orchard, 22 were from a windbreak of macadamia seedlings at the Kā'u orchard and a single selection from the Honomalino orchard (selection 900) which is apparently⁶² a hybrid. These orchards were established from the late 1940s, with otherwise grafted trees. No record is available of the source and pedigree of these seedlings. These selections are referred to as *Keaau #* or *Kau #* in publications, not to be confused with the cultivars *Keaau* and *Kau* (see below). There is no evidence that these newer selections have any relationship to the older named cultivars.

Released cultivars and elite selections

The initial cultivars released by UH arose from the 1936 selection program. The first five cultivars from the UH selection program were released in 1948: *Keauhou* (HAES selection 246), *Nuuanu* (336), *Kohala* (386), *Pahau* (425) and *Keakea* (508) (Storey 1948; Storey and Hamilton 1948). All except *Keauhou* were selections made from the Nutridge orchard (Fig. 1). Hawai'ian names were used to associate them with their Hawai'ian origin (Shigeura and Ooka 1984; Storey 1948, 1963). Hardner et al. (2009) incorrectly reported 226 was the UH selection number for *Nuuanu* (correctly 336) and that the Keauhou orchard was the source of *Nuuanu*, *Kohala* and *Pahau*. To support the adoption of the new cultivars, UH propagated and distributed the cultivars to nurseries and growers (Storey and Hamilton 1948).

By 1952, information from ongoing cultivar field trials indicated *Nuuanu*, *Kohala* and *Pahau* were not suitable for commercial production (Hamilton et al. 1952). It was suggested⁶³ the recommendation of the first five cultivars (Storey 1948) was based on observation from only a few individual trees on experiment stations at Kaua'i, Kona, and Haleakalā on Maui. Two additional cultivars, *Ikaika* (333) and *Wailua* (475), both also selected in 1936 from Nutridge (Fig. 1), were released in 1952, based on

⁵⁹ UH macadamia selection records. *Op. cit.*

⁶⁰ Marc Meisner farm manager UH Kainalu-Kona ES 10th June 2013 Personal communication.

⁶¹ UH macadamia selection records. *Op. cit.*

⁶² Observed by Author 10th June 2013.

⁶³ Lau *Op. cit.*

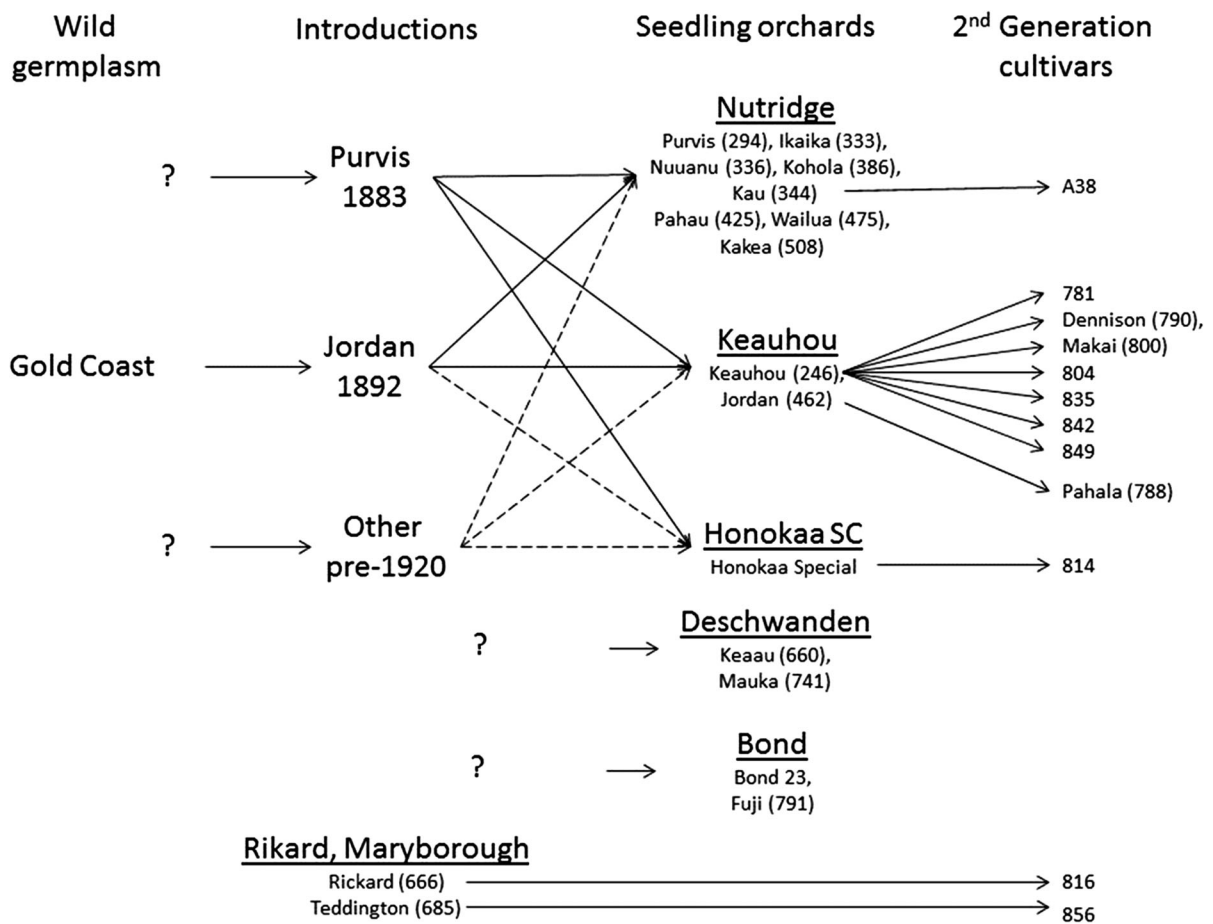


Fig. 1 Reconstructed pedigree of named cultivars and commercially deployed selections from Hawai'i

this field trial information (Hamilton et al. 1952). The cultivar *Wailua* was considered a hybrid (Hamilton and Fukunaga 1973). Storey and Hamilton (1954) consider these early cultivars are similar in nut and kernel characteristics, but adapted to different elevation and local environmental conditions. It has been suggested⁶⁴ the cultivar *Keauhou* (246) performed poorly in orchards at Hilo, Pāhala and Honokā'a, but was better suited to Kona.

Selection 462 from the 1936 survey of the Keauhou orchard (Fig. 1) was named by the California Macadamia Society as *Jordan* (Brooks 1978; Storey 1968). It is unknown how and when *Jordan* was introduced into California, although it may have been

one of those introduced in 1962 (Westree 1963). Another selection, 406, also from the 1936 survey of the Keauhou orchard, was recommended for use as a rootstock, mainly because of the thin shell (Storey and Hamilton 1948).⁶⁵

In 1971, *Kau* (344) was released (Hamilton and Nakamura 1971). This cultivar was originally selected from the Nutridge orchard in 1936 (Fig. 1). The selection was grafted in 1938, however, only two trees were planted in a trial at the UH Kainaliu-Kona Experiment Station and these did not perform well (Hamilton and Nakamura 1971). The original tree was rediscovered in a 1955 survey of the Nutridge orchard and performed better when re-propagated and trialed more extensively (Hamilton and Nakamura 1971).

⁶⁴ Chase S. Transcript of interview with George Schattauer 1989. Hawai'iian Macadamia Nut Industry Records, Series No. AR14. Held at Lyman Museum Archives, Hilo.

⁶⁵ Stewart *Op. cit.*

Keaau (660) was selected from the Deschwanden orchard in Lāwa‘i Valley on Kaua‘i in 1948, and released in 1962 (Hamilton and Ooka 1966). There is some confusion of the source of this selection in subsequent literature, possibly because Hamilton and Ooka (1966) indicate the orchard was operated by Glaisyer. However, there is no record⁶⁶ that Glaisyer ever owned this land.

The cultivar *Mauka* (741, Hamilton and Ito 1977) was selected in 1957. Hamilton and Ito (1977) report *Mauka* was a seedling tree in the Glaisyer orchard in Lāwa‘i Valley on Kaua‘i, but also indicate *Mauka* was selected from the same orchard as *Keaau*. UH selection records⁶⁷ confirm the Deschwanden orchard as the source of *Mauka*. Interestingly, *Keaau* (selected 1948) and *Mauka* (selected 1957) were both given the same tree number (#3) in the UH selection records,⁶⁸ as were selections 559 and 740 (#2).

The cultivar *Pahala* (788) was the first of the advanced generations selections and an OP progeny of *Jordan* (462) (Fig. 1) (Table 2). This parentage is confirmed by UH selection records.⁶⁹ There has been some confusion in the literature of the parentage of this cultivar as some authors (Aradhyia et al. 1998; Steiger et al. 2003) have attributed it to *Keauhou* (246). Steiger et al. (2003) also reports *Pahala* was named in 1981, possibly confusing this with the selection year (Table 2). Copper (1990) reported that *Yonik*, an Israeli cultivar, was a sport of *Pahala*.

The cultivars *Makai* (800) (Hamilton and Ito 1977) and *Dennison* (790) (Hamilton and Ito 1990) are OP progeny of *Keauhou* (246) (Fig. 1) (Table 2). *Dennison* was the last named Hawai‘ian cultivar.

The UH selection records⁷⁰ also give the pedigree of several important un-named Hawai‘ian selections that have been planted in commercial orchards, particularly in Australia (Fig. 1; Table 2). Many are OP progeny of *Keauhou* (246), while the parentage of other cultivars include *Honokaa Special* (see below for origin) and two Australian selections introduced in the 1950s (*Rikard* and *Teddington*). These selection records substantiate results from Peace (2005) who,

using DNA marker analysis, deduced *Keauhou* (246) was the mother of selections 783 and 828.

The Australian selection *NSW44*, introduced into Hawai‘i and given the UH selection number 695, was later named in California as the cultivar *Beaumont* (Storey 1965). This selection was rejected by UH in 1962 (Hamilton and Fukunaga 1962b; Storey 1965).

The cultivar *Fuji* (791) was selected in 1964,⁷¹ but initially named as *Richard* in South Africa (Blight 1989). The name was changed to *Fuji* by Hawai‘ian breeders who had originally made the selection (Peace 2005). There is no evidence of any relationship between *Fuji* and *Rickard*, an older Australian selection introduced into Hawai‘i in the 1950s (Hardner et al. 2009). DNA marker evidence indicates one of the grandparents of *Fuji* was a *M. ternifolia* individual (Peace et al. 2005) and these authors suggest the reduced stature and thin shells of this cultivar may have been derived from the *M. ternifolia* ancestor. There are no known reports of *Fuji* producing bitter kernels. The name Kunio Fujii is associated with the entry for 791 in the UH selection records.⁷² Mr. Fujii was an employee of UH at Mealani Experiment Station on the island of Hawai‘i between 1964 and 1992, and recalls⁷³ transferring scion wood he thought had been collected from the Bond orchard as *Bond Special* to the UH selection program. No other records of *Bond Special* have been found.

Other Hawai‘ian selections

Initially, HSC collaborated with UH to survey their seedling orchards for elite individuals (Wagner-Wright 1995). However, complications arose and HSC later denied access to selections from their orchards (Beaumont 1939a).^{74,75}

Seven selections (A19-28, B-4, A48-3, C37-60, B5-6, N-1 and B27-5) were recorded from surveys of approximately 25,000 seedlings in HSC orchards (Wagner-Wright 1995).⁷⁶ The selection C37-60 appears to be the cultivar *Honokaa Special* (Hamilton

⁶⁶ Property tax land appraisal cards for Tax Map Key 2-5-2-37 held on microfilm by county of Ka‘ūa‘i, Līhu‘e.

⁶⁷ UH macadamia selection records. Held at USDA-ARS Hilo.

⁶⁸ UH *Op. cit.*

⁶⁹ UH *Op. cit.*

⁷⁰ UH *Op. cit.*

⁷¹ UH *Op. cit.*

⁷² UH macadamia selection records. Held at USDA-ARS Hilo.

⁷³ Kunio Fujii Personal communication 9th July 2013 retired UH.

⁷⁴ Stewart *Op. cit.*

⁷⁵ Wagner-Wright *Op. cit.*

⁷⁶ Stewart *Op. cit.*

Table 2 Details of UH/HAES advanced generation selections in including UH/HAES selection number (#), year selected (yr), identity of parent and location of original seedling of selection

Selection name	UH/HAES #	yr	Parent name	UH/HAES #	Location	Ref.
<i>Pahala</i>	788	1963	<i>Jordan</i>	462	UH Poamoho RS	a, b
<i>Makai</i>	800	1967	<i>Keauhou</i>	246	UH Waiākea ES	c, b
<i>Dennison</i>	790	1963	<i>Keauhou</i>	246	UH Waimānalo RS	d, b
	781	1963	<i>Keauhou</i>	246	UH Waimānalo RS	b
	804	1967	<i>Keauhou</i>	246	UH Poamoho RS	b
	835	1969	<i>Keauhou</i>	246	UH Malama-kī ES	b
	842	1971	<i>Keauhou</i>	246	UH Waiākea ES	b
	849	1973	<i>Keauhou</i>	246	UH Waiākea ES	b
	814	1969	<i>Honokaa Special</i>		UH Malama-kī ES	b
	816	1969	<i>Rikard</i>	666	UH Malama-kī ES	b
	856	1974	<i>Teddington</i>	685	UH Hāmākua ES ^e	b
	783	1963	<i>Keauhou</i>	246	UH Waimānalo RS	b
	828	1969	<i>Keauhou</i>	246	UH Waiākea ES	b

^a Hamilton et al. (1981)

^b UH macadamia selection book. Held at UH Hilo

^c Hamilton and Ito (1977)

^d Hamilton and Ito (1990)

^e No record of seedling selection trial at this location

and Fukunaga 1973)⁷⁷ selected from the Kapulena seedling orchard.⁷⁸ *Honokaa Special* was reportedly (Hamilton and Ito 1976) selected under the UH selection program, but no reference to this name, or the selection names used by HSC, are found in the UH selection records.⁷⁹ *Honokaa Special* is considered^{80,81} wind resistant because the branches are more flexible than UH cultivars. It was planted almost exclusively in HSC clonal orchards (Hamilton and Fukunaga 1970, 1973; Hamilton and Ito 1976), although Hamilton⁸² reports *Honokaa Special* was also planted at MacFarms Honomolino Orchard. Beaumont (1958) suggests *Honokaa Special* was

derived from the Purvis introduction, supported by others⁸³ who suggest the lineage of HSC cultivars could be traced back to the Purvis introduction. Alternatively, it may be *Honokaa Special* is the elite selection produced from seed imported by HSC from Australia referred to by Thevenin (1947).

The cultivar *Bond 23* was a *M. integrifolia* selection from the 1920s Bond seedling orchard (Shigeura and Ooka 1984).⁸⁴ Kernels produced by this cultivar were considered (Shigeura and Ooka 1984) to be of high quality, although this is contradicted by Hamilton.⁸⁵ Little other information was found on the utilisation of *Bond 23*, although it was used extensively in the Bond clonal orchards⁸⁶ and was favoured as a rootstock (Wagner-Wright 1989). As reported above, apparently the cultivar *Fuji* (791) was collected as the cultivar *Bond Special*. No evidence is available to clarify the relationship between *Bond 23* and *Bond Special*.

⁷⁷ Stewart *Op. cit.*

⁷⁸ Robert DeRego Personal communication 30/5/2015 retired employee HSC.

⁷⁹ UH macadamia selection records. *Op. cit.*

⁸⁰ DeRego *Op. cit.*

⁸¹ Stewart *Op. cit.*

⁸² Wagner-Wright *Op. cit.*

⁸³ Hamilton *Op. cit.*

⁸⁴ Wagner-Wright *Op. cit.*

⁸⁵ *Op. cit.*

⁸⁶ Trump J. 5th July 2013 Personal communication.

A minor cultivar *Chong 6* was reportedly (Hamilton and Fukunaga 1970; Hamilton and Ito 1976) planted on a limited scale in the Kohala Sugar Company orchards. Hamilton and Ito (1976) report that this cultivar was selected in the UH program, but no information to connect this name to a selection number has been found.

Contribution of germplasm to cultivars

The Jordan introduction is considered by many (Beaumont 1958; Hamilton and Ito 1986; Hamilton and Young 1966)⁸⁷ to be the primary source of the Hawai'ian cultivars. The Purvis germplasm was considered inferior, partly because it may have contained some *M. ternifolia* germplasm (Pope 1929c), and the Jordan germplasm produced nuts with higher kernel recovery (Wagner-Wright 1995) and superior quality kernels (Crawford 1937; Storey 1957). The Purvis introduction is considered by Beaumont (1958) to have only produced a single commercial cultivar, *Honokaa Special* (but see above).

Comparison with results from molecular studies

Results from a number of studies employing molecular markers to describe the genetic variation among macadamia cultivars and selections are generally consistent with the relationships described above using historical records. No difference between the cultivars *Keaau* and *Mauka* was detected in two studies employing independent microsatellites (12 loci for Nock et al. 2014; 6 loci for Peace et al. 2004). However, in the (Peace et al. 2004) study, *Keauhou* and *Makai* (which from records share a parent-offspring relationship) are more dissimilar than *Makai* and *Kau*, and *Keauhou* and *Ikaika*, *Kekea*, and selection 816, although the relationships among these individuals are unknown. Limited genetic variation was also detected between these cultivars using eight co-dominant isozyme (Aradhya et al. 1998), 105 dominant AFLP (Steiger et al. 2003), 165 dominant RAF (Peace et al. 2005) or 23 co-dominant and 173 dominant RAMiFi (Peace et al. 2005, 2008) markers, and is less than any other pairwise comparisons.

Keauhou and *Makai* are also closely clustered in three of these studies (Aradhya et al. 1998; Peace et al. 2004, 2005), but do not appear more genetically similar than other pairwise comparison in the AFLP study (Steiger et al. 2003). While *Keaau* and *Mauka* (and *Keauhou* and *Makai*) are clustered together based on RAPD marker variation (Peace et al. 2004), they are more dissimilar than *A4* and *A16* (which are at least half-sibs, and probably full sibs, Hardner et al. 2009). It is unknown to what degree scoring error contributed to the genetic variation observed in these later studies, however, these results provide strong support for the conclusion *Keaau* and *Mauka* are genetically very similar. Although the same tree number in the Deschwanden orchard is recorded for each of the cultivars, further work is needed to support the conclusion *Keaau* and *Mauka* are the same clone.

M. ternifolia in Hawai'i

There are numerous pieces of evidence suggesting germplasm of what is currently classified as *M. ternifolia* was introduced in Hawai'i at some stage. Pope (1929b) argues the seed Purvis introduced was from *M. ternifolia*, as Forbes (1928b) described the kernels produced by these trees as small and not appealing (however see above for further discussion). In addition, Pope (1929b) noted bitter kernels had been produced by seedlings growing in the Kona district that had been sourced from the region in which the Purvis introduction was grown. Others reported the production of small bitter kernels from backyard trees (Young and Hamilton 1966), trees in seedling orchards at Hō'ae'ae Ranch (Pope 1929b) and unspecified locations (Ripperton and Edwards 1932), and in some (Waimea, Momohara) orchards in the Kalāheo district on Kaua'i (Hamilton and Young 1966; Shigeura and Ooka 1984),⁸⁸ including selection 736 that had been sourced from the Momohara orchard (Hamilton and Young 1966). It has been reported (Moltzau 1939; Shigeura and Ooka 1984)^{89,90} most of these trees were subsequently removed to reduce the risk that bitter kernels—that could not be detected

⁸⁷ Stewart *Op. cit.*

⁸⁸ Takahashi *Op. cit.*

⁸⁹ Lau *Op. cit.*

⁹⁰ Takahashi *Op. cit.*

until consumed—would contaminate commercial consignments.

DNA marker research has also demonstrated approximately ¼ of the genome of the cultivar *Fuji* (791) contains *M. ternifolia* specific alleles (Peace et al. 2005). There is little evidence bitter kernels are produced by pure *M. integrifolia* or *M. tetraphylla* individuals, although a kernel with traces of bitterness was reported from the *M. integrifolia* × *tetraphylla* hybrid cultivar Beaumont.⁹¹ Preliminary experiments with interspecific crossing indicate kernel bitterness is recessive (Hardner et al. 2000), suggesting interspecific hybrids between *M. ternifolia* and *M. integrifolia* are unlikely to produce bitter kernels unless dominance is incomplete. However, it may be possible a bitter kernel producing double recessive genotype could arise from a cross between interspecific hybrids suggesting at some stage either pure *M. ternifolia* or *M. integrifolia* × *ternifolia* hybrids were introduced into Hawai'i.

Conclusions

This review has clarified many issues of the domestication pathway of macadamia in Hawai'i from introduction in the late nineteenth century to production of cultivars and advanced selections that dominate current world production. Inconsistencies in the published literature have been identified and, where possible, resolved or greater historical detail added to reduce uncertainty. However, the origin of the Purvis introduction remains unknown and questions are raised about the currently accepted Australian origin of the Jordan introduction. An additional significant introduction of macadamia in the early part of the twentieth century is identified, but its relevance to domesticated germplasm is unknown. There is also strong evidence that *M. ternifolia* germplasm was introduced into Hawai'i at some stage. Early plantings of seedling production orchards that are samples of the available germplasm in Hawai'i during the early stages of domestication have been documented. Knowledge of the origin and genetic structure of the early Hawai'ian introductions could be improved if remnants of these plantings could be

located and sampled for subsequent DNA analysis. The preference for *M. integrifolia* defined in the early phase of the Hawai'ian industry due to the apparent poor quality of *M. tetraphylla* kernels may be in part due to the use of kernels collected from poorly managed orchards of *M. tetraphylla* in these evaluations and possibly inferior germplasm introduced into Hawai'i. This suggests that *M. tetraphylla* may provide an additional source of valuable germplasm for genetic improvement of this crop. Similar to the history of many other crops, mastering vegetative propagation appears to be one of the major drivers of the rapid domestication of macadamia. The strategy employed by the UH selection program of using phenotypic performance of individual seedlings to select candidates for further evaluation in clonal plantings has produced elite cultivars, however the failure of a large number of the early cultivars demonstrates that use of phenotypic information from a single seedling for selection is not highly accurate. The pedigrees of advanced selections have been clarified and the high frequency of commercial selections that are offspring of *Keauhou* suggests that the genetic base of these selections is narrow, and widening the diversity of parents is required to avoid deleterious effects of inbreeding depression and maximise selection response. In addition, improved definition of the pedigree of macadamia selections used as parents in advanced breeding programs will improve the accuracy of breeding and clonal value prediction from the analysis of their progeny.

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⁹¹ UH macadamia selection records. *Op. cit.*

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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